

# Improving Estimation of Wolf Recruitment and Abundance, and Development of an Adaptive Harvest Program for Wolves in Montana



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**Sarah Sells & Allison Kever**

PhD Students

Montana Cooperative Wildlife Research Unit  
205 Natural Sciences, Missoula, MT 59812

**Justin Gude**

Res & Tech Services Bureau Chief  
Montana Fish, Wildlife and Parks  
1420 E. 6<sup>th</sup> St., Helena, MT 59620

**Mike Mitchell**

Unit Leader

Montana Cooperative Wildlife Research Unit  
205 Natural Sciences, Missoula, MT 59812

**Kevin Podruzny**

Biometrician

Montana Fish, Wildlife and Parks  
1420 E. 6<sup>th</sup> St., Helena, MT 59620



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## **INTRODUCTION**

Wolves (*Canis lupus*) began recolonizing northwestern Montana by 1979, and were reintroduced to Yellowstone National Park and central Idaho in 1995 and 1996 (Bangs and Fritts 1996). After rapid population growth, they were delisted from the endangered species list in 2011. Since that time, Montana has agreed to maintain populations and breeding pairs (a male and female wolf with 2 surviving pups by December 31; USFWS 1994) above established minimums ( $\geq 150$  wolves and  $\geq 15$  breeding pairs within each state). Montana estimates population size every year using patch occupancy models (POM; MacKenzie et al. 2002, Rich et al. 2013, Miller et al. 2013, Bradley et al. 2015), however, these estimates are sensitive to pack size and territory size, and were developed pre-harvest. Reliability of future estimates based on POM will be contingent on accurate information on territory size, overlap, and pack size, which are expected to be strongly affected by harvest. Additionally, breeding pairs, which has proven to be an ineffective measure of recruitment, are determined via direct counts. Federal funding for wolf monitoring is decreasing now that wolves are delisted, and future monitoring will not be able to rely on intensive counts of the wolf population. Furthermore, monitoring has become cumbersome and less effective since the population has grown. With the implementation of harvest, it is pertinent to predict the effects of harvest on the wolf population and continue to monitor to determine effectiveness of management actions to make informed decisions regarding harvest and trapping quotas.

## **STUDY OBJECTIVES**

Our 4 study objectives are to:

1. Improve estimation of recruitment.
2. Improve and maintain calibration of wolf abundance estimates generated through POM.
3. Develop framework for dynamic, adaptive harvest management based on achievement of objectives 1 & 2.
4. Design targeted monitoring program to provide info needed for robust estimates and reduce uncertainty in the AHM paradigm over time.

Two PhD students are addressing the 4 study objectives as part of Project 1 (Sarah Sells) and Project 2 (Allison Keever; Fig. 1).

## **DELIVERABLES**

1. A method to estimate recruitment for Montana's wolf population that is more cost effective and biologically sound than the breeding pair metric.

2. A model to estimate territory size and pack size that can keep POM estimates calibrated to changing environmental and management conditions for wolves in Montana.
3. An adaptive harvest management model that allows the formal assessment of various harvest regimes and reduces uncertainty over time to facilitate adaptive management of wolves.
4. A recommended monitoring program for wolves to maintain calibration of POM estimates, determine effectiveness of management actions, and facilitate learning in an adaptive framework.

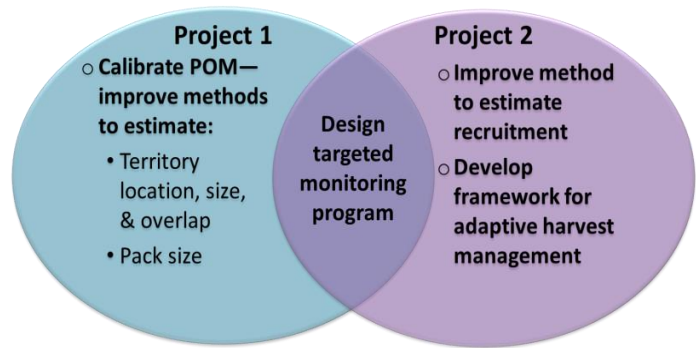


Fig. 1. Objectives for this project are being addressed under 2 separate projects.

## LOCATION

This study encompasses wolf distribution in Montana and Idaho.

## STUDY PROGRESS

We began our PhD projects in January 2015 (Fig. 2). Much of year 1 was devoted to literature reviews on animal behavior, carnivores, modeling, optimal foraging, etc. and determining approaches for our dissertations. We also formed and held multiple meetings with our committees, completed more coursework, and finalized research statements. Additional efforts focused on communicating with wolf specialists, identifying target packs for collaring, managing collar orders and data, and helping coordinate contracts and capture plans for winter aerial captures for January and February 2016. We also met with wolf specialists in the field to learn more about the wolves in their regions, and coordinated and held meetings with the specialists to plan future project efforts. Our dissertation proposals are currently underway as of spring 2016, which we will defend at the end of spring semester.

Based on these efforts, we have formulated a general rationale and analytical approach that will facilitate achieving the project objectives, which is detailed in the below sections.

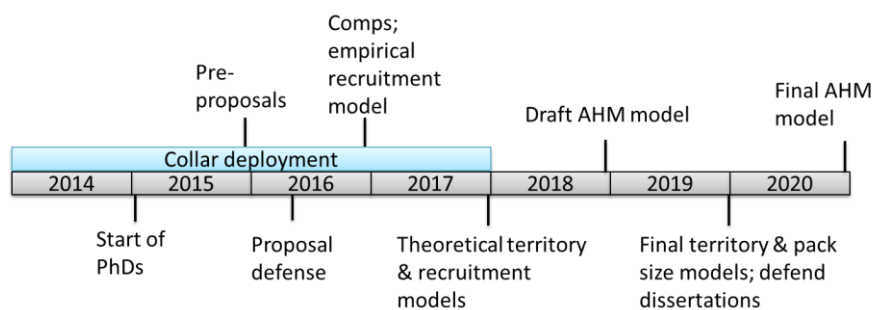


Fig. 2. Project timeline for PhD dissertations.

As of February 2016, 35 collars have been purchased for this project, and 2 additional are being shared among MFWP projects. MFWP field staff has successfully captured 40 wolves, deploying 10 collars in 2014, 14 collars in 2015, and 16 collars as of February 2016. Eight mortalities have occurred (5 by harvest, 1 by vehicle, 1 presumed by vehicle, and 1 from capture) and the status of 1 collared wolf remains unknown due to collar failure, mortality, or distant dispersal. Additional capture efforts will continue through ground and aerial capture efforts through 2017.

## **FUTURE APPROACHES AND RATIONALE**

### **Objective 1: Improve estimation of recruitment.**

*Allison Keever*

Estimating recruitment (i.e., number of young produced that survive to an age at which they contribute to the population) of wolves can be difficult due to their complex social structure. Wolves are cooperative breeders, and pack dynamics (e.g., pack tenure, breeder turnover, and number of non-breeding helpers) can affect recruitment and pup survival (e.g., Ausband et al. 2015, Borg et al. 2015). Cooperative breeding oftentimes relies on the presence of non-breeding individuals that help raise offspring (Solomon and French 1997), and reduction in group size can lead to decreased recruitment in cooperative breeders (Sparkman et al. 2011, Stahler et al. 2013). Human-caused mortality through both direct and indirect means (Ausband et al. 2015) and prey biomass per wolf (Boertje and Stephenson 1992) have been shown to affect recruitment. It will be important to consider the effects of harvest, pack dynamics, wolf density, and prey availability on recruitment.

Recruitment estimation is further hindered by the size of the wolf population and the large scale over which recruitment is needed. Currently, MFWP documents recruitment in wolves by visual counts of breeding pairs (a male and female wolf with 2 surviving pups by December 31; USFWS 1994). These counts, however, are likely incomplete due to the size of the wolf population and limited resources. A breeding pair estimator (Mitchell et al. 2008) could be used to estimate breeding pairs, however the breeding pair estimator requires knowing all pack sizes, data that are hard to collect given the size of the current wolf population. Federal funding for wolf monitoring is decreasing now that wolves are delisted, and future monitoring will not be able to rely on intensive counts of the wolf population. Additionally, the breeding pair metric is an ineffective measure of recruitment, as it gives little insight into population growth rate or the level of harvest that could be sustained. Recruitment could be estimated by comparing visual counts at the den site to winter counts via aerial telemetry (Mech et al. 1998) or by marking pups at den sites (Mills et al. 2008). An alternative method could include non-invasive genetic sampling (Ausband et al. 2015) at predicted rendezvous sites (Ausband et al. 2010). These methods, however, may not be feasible on large scales due to budget and staff constraints.

## Approach

My objective is to develop an approach to estimate recruitment that is more tractable, cost effective, and biologically credible than the breeding pair metric. To do this I will focus on developing an accurate method to estimate recruitment for wolves. I will test an empirical, per capita recruitment model which will be built off of data collected for wolves in Montana and Idaho using generalized linear models. The data include numbers of packs and wolves estimated from POM and actual wolf counts, including pups, from wolf surveys conducted annually. A per capita model, however, may not be the most accurate way to predict recruitment in wolves due to their social nature, and an empirical model may require data which will be difficult to collect in the future. I will also develop and test a theoretical recruitment model which will build off of existing work on pup survival and recruitment (e.g., Sparkman et al. 2011, Stahler et al. 2013, Ausband et al. 2015, Borg et al. 2015). The theoretical model will build off of relationships found between recruitment, group size, and harvest in cooperative breeders (e.g., Sparkman et al. 2011, Stahler et al. 2013, Ausband et al. 2015, Borg et al. 2015). After constructing multiple, competing theoretical models about what is important for recruitment I will test them against actual data on recruitment to determine which model has most support. I will compare the best theoretical model with the empirical model to determine which predicts recruitment most accurately and which requires the least amount of data and can be employed within budgetary and staff time constraints.

## **Objective 2: Improve and maintain calibration of wolf abundance estimates generated through POM.**

*Sarah Sells*

Monitoring is a critical, yet challenging, management tool for gray wolves. Monitoring helps MFWP set and fulfill management objectives for minimum populations and harvest levels. Results also facilitate communicate with stakeholders and the public. Monitoring any large carnivore is challenging, however, due to their elusive nature and naturally low densities (Boitani et al. 2012). This is particularly true for wolves due to increasing populations, decreasing funding for monitoring, and changing behavioral dynamics with harvest.

Abundance estimates are a key component of monitoring (Bradley et al. 2015). Abundance is estimated with 3 parameters: area occupied, average territory size, and annual average pack size (Fig. 3, Bradley et al. 2015). Area occupied is estimated with a Patch Occupancy Model (POM) based on hunter observations and field surveys (Miller et al. 2013, Bradley et al. 2015). Average territory size is assumed to be 600 km<sup>2</sup> with minimal overlap, based on past work (Rich et al. 2012). Annual average pack size is estimated from monitoring results. Total abundance (N) is then calculated as:  $N = (\text{area occupied} / \bar{x} \text{ territory size}) \times \bar{x} \text{ pack size}$ .

Whereas estimates of area occupied from POM are expected to be reliable (Miller et al. 2013, Bradley et al. 2015), reliability of abundance estimates hinge on key assumptions about territory

size, territory overlap, and pack size (Bradley et al. 2015). Assumptions of fixed territory size and minimal overlap are simplistic; in reality, territories vary spatiotemporally (Uboni et al. 2015). This variability is likely even greater under harvest (Brainerd et al. 2008). Meanwhile, pack size estimates rely on locating and accurately counting packs each year, which is increasingly difficult due to the number of packs and declining funding for monitoring (Bradley et al. 2015).

Since implementation of harvest in 2009, several factors have further compounded these challenges and decreased accuracy of pack size estimates. First, whereas larger packs are generally easier to find and monitor, average pack size has decreased under harvest (Bradley et al. 2015). Difficult-to-detect smaller packs may be more likely to be missed altogether, biasing estimates of average pack size. Harvest and depredation removals also affect social and dispersal behavior (Adams et al. 2008, Brainerd et al. 2008, Borg et al. 2014, Ausband 2015). Additionally, pack turnover is now greater than in populations with less human-caused mortality.

Development of reliable methods to estimate territory size, territory overlap, and pack size is critical for accurate estimates of abundance. Theoretical models for wolf behavior would provide predictions that can be compared to real data to identify the models with most support. Resulting models would yield reliable scientific inference and be predictive at any spatiotemporal scale. Importantly, abundant data would not be required for predictions.

## Approach

My goal is to develop models to estimate territory and group size of wolves to calibrate estimates of abundance in Montana and Idaho. I will draw on theory and previous research to construct theoretical models for territories and group sizes of wolves. I will then conduct simulations to generate predictions, which I will test on locations and group sizes of actual packs. The models I develop will be predictive at any spatiotemporal scale in absence of abundant empirical data. Alongside POM, the models will help accurately estimate abundance of wolves through biologically based, spatially explicit predictions for territory size, location, and overlap and group size.

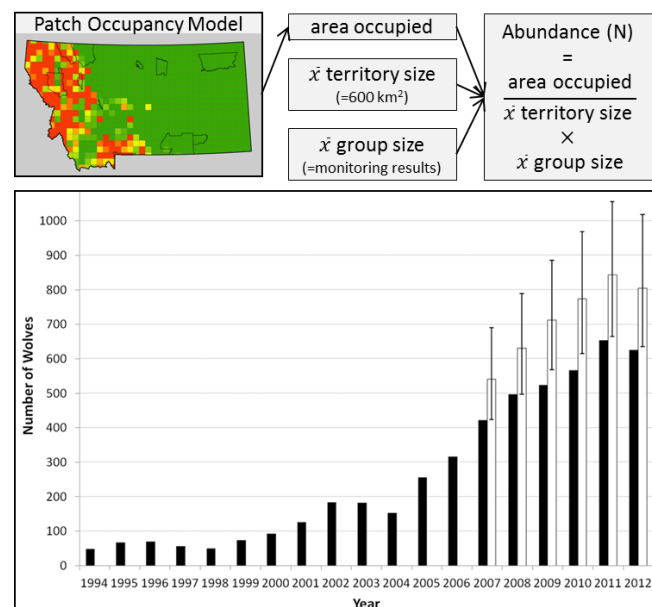


Fig. 3. Example of POM results (red indicates highest occupancy probability, green lowest), and methods for calculating abundance. Graphed abundance since 1994 is based on minimum counts (black bars) and POM-based estimates (white bars). (Adapted from Bradley et al. 2015.)

Data will come from multiple sources. MFWP will deploy  $\leq 20$  GPS collars per year from 2014–2017 to collect locations on wolf packs. I will also include data from GPS-collared wolves in Idaho to increase our sample size. Additionally, I will use existing data from VHF and GPS-collared wolves from past years (potentially 1995–current). I will use pack size estimates collected through monitoring efforts.

### **Objective 3: Develop framework for adaptive harvest management.**

*Allison Kever*

Wolves have been harvested in Montana since they were delisted. In 2011 there was a statewide wolf quota of 220 which was divided into 14 wolf management units (Bradley et al. 2015). Since that time the statewide quota has been discontinued, a five wolf bag limit was put in place, and season length and timing has changed (Bradley et al. 2015).

Although hunting and trapping continues to be an important tool for wolf management, there is debate about the effects of harvest on wolf populations (e.g., Creel and Rotella 2012, Gude et al. 2012). Creel and Rotella (2010) found that human-caused mortality was not compensated for and was potentially super-additive. The human-caused mortality they considered, however, was largely from control removals in unharvested populations, and hunting and trapping will likely have different effects on population growth (Haber 1996). Furthermore, Creel and Rotella (2010) only tested compensation in survival, and recruitment and dispersal are known to be very important for wolf population dynamics (Adams et al. 2008, Gude et al. 2012). There is a lot of variation in the reported level of harvest wolf populations can sustain before growth rate decreases (Mech 2001, Adams et al. 2008, Creel and Rotella 2010, Gude et al. 2012), however the reasons behind this variation have not been explored. This variation could be due to different types and timing of human-caused mortality due to the effects of breeder loss on recruitment (Borg et al. 2015), differences in prey availability and consumption as prey availability is important for wolf population growth rate (Vucetich and Peterson 2004), or differences in scale and methodology of data collection and analysis. There is additional uncertainty about the role of density dependence in wolf population dynamics (Cariappa et al. 2011, Cubaynes et al. 2014, McRoberts and Mech 2014).

Given uncertainty in wolf population dynamics and the effects of harvest on those dynamics, it is difficult to make informed harvest decisions that have a high likelihood of achieving the desired outcome. Despite uncertainty, harvest decisions must still be made. This leads to the question of how do decision-makers make the best decision with what data are available, and how do we gather information to improve decision making? Adaptive management is a tool that can help guide management when there are iterated decisions (e.g., annual harvest recommendations) while accounting for and reducing uncertainty over time (Walters 1986, Williams et al. 2009). Adaptive management is a structured approach to making decisions that is transparent and repeatable, and when applied to harvest is termed adaptive harvest management (AHM). An

AHM model for wolves will allow the formal assessment of harvest regimes in meeting objectives and determination of underlying biological processes.

## Approach

My objective is to develop an adaptive harvest management (AHM) model for wolves to help guide harvest decisions while learning about the effects of harvest on wolves through management. Developing an AHM model requires 4 components: 1) objectives, 2) alternative management actions, 3) a model of the natural resource system to predict the effects of management, and 4) a monitoring program that allows decision-makers to determine the effectiveness of those management actions, reduce uncertainty, and learn over time. Objectives, the first component of AHM, are how one would measure success of management actions. The second component, alternative management actions, is used to determine the optimal set of decisions which can affect the system model to meet objectives. A system model (the third component; e.g., model of population dynamics) predicts the current system state, for example population size. The system model can incorporate different types of uncertainty within the model or by having alternative system models about system dynamics. Comparing predictions from alternative system models to monitoring data (fourth component of AHM) reduces uncertainty, and Bayes theorem is used to update model support, or likelihood, which influences future decisions.

Objectives: Prior work outlining objectives for wolf management was completed in 2010 with MFWP. The objectives produced by this work were to maximize sustainability of the wolf population, maximize sustainability of ungulate populations, and maximize public satisfaction. I developed an objectives hierarchy adapted from the 2010 objectives which links the fundamental objectives, those deemed most important, to means objectives which outline how to achieve the fundamental objective (Fig. 4). I will use the objectives outlined in the 2010 wolf management workshop for the AHM model for wolves.



Fig. 4. Objectives hierarchy developed from the 2010 wolf management structured decision making workshop. The blue boxes represent the fundamental objectives which are most important, and the green boxes represent the means objectives for achieving the fundamental objectives.



Alternative management actions: I will develop alternative management actions (harvest scenarios) in conjunction with MFWP. Although MFWP recommends harvest regulations to the Montana Fish and Wildlife Commission they cannot prescribe actual harvest rates, so I will predict harvest rates across the state. I will use data on hunter & trapper effort and hunter & trapper success to test how harvest rates have changed with changing regulations.

System model: I will develop and test a system model (population model in this case) for wolf population dynamics that can be informed by data from a feasible monitoring program. The population model will describe the effects of harvest on wolf population dynamics. I will test the population model by comparing model predictions of population size to estimates from POM and wolf counts.

Monitoring program: Monitoring is an essential component to AHM, as that is how learning occurs. Monitoring data are used to update the AHM model to reduce uncertainty through time. After the AHM model is complete, I will conduct a sensitivity analysis (Clemen and Reilly 2001) to determine the influence of each type of monitoring data on decision making. This will allow us to target areas where more data should be collected in order to improve decision making over time. A monitoring program for wolves must also continue to include estimates of population size from POM to evaluate effectiveness of management actions.

To develop the complete AHM model, I will combine the above components and determine the optimal harvest strategy given objectives for wolf management. I will estimate harvest strategies for each population size using simulation optimization methods (Fu et al. 2005, Lin et al. 2013) and objectives outlined by MFWP. I will estimate optimal harvest strategies for alternative population models (e.g., compensatory vs. additive mortality and density dependence vs. independence) and then simulate the harvest strategies over each alternative model of population dynamics and compare model predicted population size with estimates from monitoring. Alternative model predictions that are closest to estimates from monitoring will gain support for models, and model support will be updated through Bayes theorem. Support for any one alternative model is not static, and can be updated over time from observations of system states (e.g., population size). I will also evaluate the usefulness of the AHM model for management by comparing the amount of uncertainty reduced to the amount of data required to inform the model.

#### **Objective 4: Conduct sensitivity analyses & propose efficient monitoring regime.**

*Allison Keever and Sarah Sells*

Monitoring is important for wildlife management, and a key component to adaptive management. It provides information on the starting point of the population which is used to inform a decision, and it provides a means to evaluate effectiveness of management actions and learn over time. When resources are limited, however, it is important to target monitoring as

opposed to conducting surveillance monitoring (i.e., monitoring not guided by *a priori* hypotheses that include all aspects of a population's demographic and ecological factors; Nichols and Williams 2006). Monitoring for adaptive harvest management should focus on population dynamics and harvest as those variables are likely used to determine success of achieving objectives. Using sensitivity analyses can help identify other components to target with monitoring.

### **Approach**

We will conduct sensitivity analyses (e.g., Clemen and Reilly 2001) and evaluate precision of components in each model outlined as part of this work to identify factors that strongly influence results and decisions. The components which most influence the results and lack precision can be targeted for monitoring to reduce uncertainty and produce robust population estimates. Based on results of these sensitivity analyses, we will recommend a monitoring program that will include sampling effort, sampling distribution, and what should be monitored.

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### **LITERATURE CITED**

- Adams, L. G., R. O. Stephenson, B. W. Dale, R. T. Ahgook, and D. J. Demma. 2008. Population dynamics and harvest characteristics of wolves in the Central Brooks Range, Alaska. *Wildlife Monographs* 170:1–25.
- Ausband, D. E., M. S. Mitchell, K. Doherty, P. Zager, C. M. Mack, and J. Holyan. 2010. Surveying predicted rendezvous sites to monitor gray wolf populations. *Journal of Wildlife Management* 74:1043–1049.
- Ausband, D. E., L. N. Rich, E. M. Glenn, M. S. Mitchell, P. Zagar, D. A.W. Miller, L. P. Waits, B. B. Ackerman, C. M. Mack. 2014. Monitoring gray wolf populations using multiple survey methods. *Journal of Wildlife Management* 78:335–346.

- Ausband, D. E. 2015. Groups and mortality: their effects on cooperative behavior and population growth in a social carnivore. University of Montana.
- Bangs, E. E., and S. H. Fritts. 1996. Reintroducing the gray wolf to central Idaho and Yellowstone national Park. *Wildlife Society Bulletin* 24:402–413.
- Boertje, R., and R. Stephenson. 1992. Effects of ungulate availability on wolf reproductive potential in Alaska. *Canadian Journal of Zoology* 70:2441–2443.
- Boitani, L., P. Ciucci, and A. Mortelliti. 2012. Designing carnivore surveys. Pages 8–30 *in* *Carnivore Ecology and Conservation A Handbook of Techniques*. Oxford University Press, Oxford, UK.
- Borg, B. L., S. M. Brainerd, T. J. Meier, and L. R. Prugh. 2015. Impacts of breeder loss on social structure, reproduction and population growth in a social canid. *Journal of Animal Ecology*.
- Bradley, L., J. Gude, N. Lance, K. Laudon, A. Messer, A. Nelson, G. Pauley, M. Ross, T. Smucker, and J. Steuber. 2015. Montana gray wolf conservation and management 2014 annual report. Montana Fish, Wildlife and Parks, Helena, Montana.
- Brainerd, S. M., H. Andren, E. E. Bangs, E. H. Bradley, J. A. Fontaine, W. Hall, Y. Iliopoulos, M. D. Jimenez, E. A. Jozwiak, O. Liberg, C. M. Mack, T. J. Meier, C. C. Niemeyer, H. C. Pedersen, H. Sand, R. N. Schultz, D. W. Smith, P. Wabakken, and a P. Wydeven. 2008. The effects of breeder loss on wolves. *Journal of Wildlife Management* 72:89–98.
- Cariappa, C. A., J. K. Oakleaf, W. B. Ballard, and S. W. Breck. 2011. A reappraisal of the evidence for regulation of wolf populations. *Journal of Wildlife Management* 75:726–730.
- Clemen, R. T., and T. Reilly. 2001. Making hard decisions. South-Western, Mason, Ohio.
- Creel, S., and J. J. Rotella. 2010. Meta-analysis of relationships between human offtake, total mortality and population dynamics of gray wolves (*Canis lupus*). *PLoS One* 5(9):e12918.
- Cubaynes, S., D. R. MacNulty, D. R. Stahler, K. A. Quimby, D. W. Smith, and T. Coulson. 2014. Density-dependence intraspecific aggression regulates survival in northern Yellowstone wolves (*Canis lupus*). *Journal of Animal Ecology* 83:1344–1356.
- Fu, M. C., F. W. Glover, and J. April. 2005. Glover FW, April J. Simulation optimization: a review, new developments, and applications. In: *Proceedings of the winter simulation conference*, 2005. p. 83–95.
- Glenn, E. S., L. N. Rich, and M. S. Mitchell. 2011. Estimating numbers of wolves, wolf packs, and breeding pairs in Montana using hunter survey data in patch occupancy model framework: final report. Technical report, Montana Fish, Wildlife and Parks, Helena, Montana.

- Gude, J. A., M. S. Mitchell, R. E. Russell, C. A. Sime, E. E. Bangs, L. D. Mech, and R. R. Ream. 2012. Wolf population dynamics in the U.S. Northern Rocky Mountains are affected by recruitment and human-caused mortality. *Journal of Wildlife Management* 76:108–118.
- Lin, R., M. Y. Sir, and K. S. Pasupathy. 2013. Multi-objective simulation optimization using data envelopment analysis and genetic algorithm: specific application to determining optimal resource levels in surgical services. *Omega* 41:881–892.
- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.
- McRoberts, R. E., and L. D. Mech. 2014. Wolf population regulation revisited-again. *Journal of Wildlife Management* 78:963–967.
- Mech, L. D. 2001. Managing Minnesota's recovered wolves. *Wildlife Society Bulletin* 29:70–77.
- Mech, L. D., L. G. Adams, T. J. Meier, J. W. Burch, and B. W. Dale. 1998. *The wolves of Denali*. Minnesota: University of Minnesota Press.
- Miller, D. A. W., J. D. Nichols, J. A. Gude, L. N. Rich, K. M. Podrutzny, J. E. Hines, and M. S. Mitchell. 2013. Determining Occurrence Dynamics when False Positives Occur: Estimating the Range Dynamics of Wolves from Public Survey Data. *PLoS ONE* 8.
- Mills, K. J., B. R. Patterson, and D. L. Murray. 2008. Direct estimation of early survival and movements in eastern wolf pups. *Journal of Wildlife Management* 72:949–954.
- Mitchell, M. S., D. E. Ausband, C. A. Sime, E. E. Bangs, M. Jimenez, C. M. Mack, T. J. Meier, M. S. Nadeau, and D. W. Smith. 2008. Estimation of successful breeding pairs for wolves in the U.S. northern Rocky Mountains. *Journal of Wildlife Management*. 72:881–891.
- Nichols, J. D., and B. K. Williams. 2006. Monitoring for conservation. *Trends in Ecology and Evolution* 21:668–673.
- Rich, L. N., M. S. Mitchell, J. A. Gude, and C. A. Sime. 2012. Anthropogenic mortality, intraspecific competition, and prey availability influence territory sizes of wolves in Montana. *Journal of Mammalogy* 93:722–731.
- Rich, L. N., R. E. Russell, E. M. Glenn, M. S. Mitchell, J. A. Gude, K. M. Podrutzny, C. Sime, K. Laudon, D. E. Ausband, and J. D. Nichols. 2013. Estimating occupancy and predicting numbers of gray wolf packs in Montana using hunter surveys. *Journal of Wildlife Management* 77:1280–1289.
- Solomon, N. G., and J. A. French. 1997. *Cooperative breeding in mammals*. Cambridge University Press, UK.

- Sparkman, A.M., J. Adams, A. Beyer, T. D. Steury, L. Waits, and D. L. Murray. 2011. Helper effects on pup lifetime fitness in the cooperatively breeding red wolf (*Canis rufus*). *Proceedings of the Royal Society of London, B* 278:1381–1389.
- Stahler, D. R., D. R. MacNulty, R. K. Wayne, B. VonHoldt, and D. W. Smith. 2013. The adaptive value of morphological, behavioral and life-history traits in reproductive female wolves. *The Journal of Animal Ecology* 82:222–234.
- Uboni, A., J. Vucetich, D. Stahler, and D. Smith. 2015. Interannual variability: a crucial component of space use at the territory level. *Ecology* 96:62–70.
- U.S. Fish and Wildlife Service. 1994. The reintroduction of gray wolves to Yellowstone National Park and central Idaho. Final Environmental Impact Statement. Denver, Colorado. Appendix 9.
- Vucetich, J. A., and R. O. Peterson. 2004. The influence of prey consumption and demographic stochasticity on population growth rate of Isle Royale wolves *Canis lupus*. *OIKOS* 107:309–320.
- Walters, C. J. 1986. Adaptive management of renewable resources. McMillan, New York, New York, USA.
- Williams, B. K., R. C. Szaro, and C. D. Shapiro. 2009. Adaptive management: the U.S. Department of the Interior technical guide. Adaptive Management Working Group, U.S. Department of the Interior, Washington, DC.